INFORMATION ON CHEMISTRY AND POLLINATION BIOLOGY RELEVANT TO THE SYSTEMATICS OF NEMOPHILA MENZIESII (HYDROPHYLLACEAE)

Robert W. Cruden
Department of Botany, University of Iowa, Iowa City 52240

In 1941, Constance described a paradoxical situation in *Nemophila menziesii* H. & A. s.l. The apparent contradiction involves inter-taxon sterility (Chittenden and Turrill, 1926; Rick, 1946; and Cruden, 1967) and "morphologically intermediate" flower types that suggest introgression. I present data from two divergent sources, flavonoid chemistry and pollination biology, to explore two questions: 1) whether the taxa usually included in *N. menziesii* s.l. are specifically distinct and 2) the nature and origin of variation encountered in the North Coast Ranges. First I review the distribution and floral morphology of *N. menziesii* s.l. and present data that suggest there are species-specific flavonoid profiles and that *Nemophila menziesii* s.l. is a species aggregate of three closely related species. Data obtained from a study of bees that are obligate collectors of *Nemophila* pollen corroborate the chemical data. Finally I present a model to reconcile the morphological variation, inter-taxon sterility, and specificity of *Nemophila* pollinators.

Three taxa that are closely related to *N. menziesii* s.l. and are sometimes included within it are *N. atomaria* Fisch. & Mey., *N. liniflora* Fisch. & Mey., and *N. integrifolia* (Parish) Abrams. For the purposes of this paper I refer material from San Bernardino Co. to *N. integrifolia.* Although *N. rotata* Eastw. from Point Loma, San Diego Co., and *N. integrifolia* are usually considered as synonymous (Constance, 1941; Munz, 1959), I hesitate to make the taxonomic decision to use *N. rotata,* as I have not examined the Point Loma specimens.

Nemophila menziesii s.str. (*N. insignis* Dougl. ex Benth.) is the well known baby blue-eyes. The corollas are blue with a clear white center. In the Sierra Nevada, southern California, and the South Coast Ranges the blue area reflects UV light. In the North Coast Ranges the blue area absorbs UV light. In *N. atomaria* the corolla is typically white with rows of blue-black dots radiating from its center. This species is found from Santa Clara and Santa Cruz counties, California, north to Washington Co., Oregon. The corolla absorbs UV light. The corollas of *N. liniflora* are whitish with blue to purple veins and absorb UV light. This species is found from Santa Clara Co. north to Mendocino Co., California. *Nemophila integrifolia* is a poorly understood taxon from southern California. The corollas are variable in size, range in color from deep blue to whitish, and absorb UV light.

I emphasize UV reflectivity because of its role in attracting pollinators. Bees see UV as a distinct color and the combination of UV and blue produces in the bee's eye "bee violet" (Daumer, 1958). Thus a bee can discriminate between a blue flower that reflects UV and one that absorbs UV.

Throughout most of their distributional ranges the four taxa of *Nemophila* are relatively distinct and easily differentiated. However, in the North Coast Ranges one finds, even in the same population, apparent recombination types among *menziesii, atomaria,* and *liniflora.* It is because of these "obvious" intermediates that the various taxa have been maintained as subspecies rather than species (Constance, 1941; Munz, 1959).

Floral variation is also encountered in the South Coast Ranges. Whereas typical *N. menziesii* has a clear, white center, many individuals in the South Coast Ranges have dots and dashes radiating from the center of the corolla similar to those in *N. atomaria.* Further, some populations in San Benito and Monterey counties are variable with respect to UV-reflectivity.

Chromatographic Studies

Thirty to forty corollas from each population were covered with acidified ethanol, whose volume was later reduced under vacuum. The condensed extract was spotted on 24 x 18 inch sheets of 3 MM Whatman chromatography papers. The sheets were run descending. The solvent used for the long dimension consisted of ethyl acetate; tertiary butyl alcohol; glacial acetic acid; and water (5:4:1:3 v:v). The short dimension was run in 15% acetic acid. The dried sheets were examined under UV light and UV light plus ammonia fumes. All the spots appear purple in UV light with the execption of number one (see Fig. 1), which fluoresced yellow in UV light and UV light plus ammonia fumes. In UV light plus ammonia fumes some spots remained dark (shaded spots in Fig. 1) and the other fluoresced a yellowish-green (clear spots in Fig. 1). No attempt was made to identify the various chemical compounds. The populations studied and the spots present are listed in Table 1. Three populations of *N. maculata* were studied and are included for comparison.

The populations studied fall into three distinct groups with respect to the flavonoid profiles from corolla tissue. Indeed the differences between the taxa in *N. menziesii* s.l. are as great as the differences between them and *N. maculata.* Although the number of populations sampled is small they represent a broad segment of the distributional range and morphological variation within each taxon.

Although there is intra-taxon variation with respect to most compounds, the presence or absence of particular compounds does serve to differentiate the various taxa. Without exception, *N. atomaria* lacks spots 2, 3, 15, and 16, which are usually present in *N. menziesii* and *N. integrifolia,* and with one exception its has spots 9 and 10, which are usually absent in *N. menziesii.* Likewise, *N. menziesii* lacks spots 4 and 14, which are usually present in *N. atomaria* and *N. integrifolia.* The chemical specificity is maintained even in mixed populations, e.g., at the Chiles-Pope Valley Road and Arnold Drive localities where *N. menziesii* s.str. and *N. liniflora* occurred in mixed populations.

If introgression were occurring one might anticipate its discovery in such mixed populations. Yet the chemical profiles from the Chiles-Pope Valley populations are representative of their respective taxa, and the profiles from Arnold Drive exhibit variation normally encountered in the two species. Careful comparison with other populations of the taxon in question shows that similar variation exists in populations that are geographically disjunct from the other species. For example, populations of *N. menziesii* s.str. from the Sierra Nevada lack spots 3 and 7. Likewise, the Berry Summit (Humboldt Co.) population of *N. atomaria* lacks spot 4. The lack of spot 14 in the Arnold Drive *N. atomaria (liniflora)* population is suggestive of introgression, but spot 14 is also absent from the Trinity Road (Sonoma Co.) population, which morphologically is typical *atomaria* with no evidence of introgression.

As a consequence of my work on the pollinators of *N. menziesii* s.l. (Cruden, 1972) I assumed *N. liniflora* to be a segregate of *N. atomaria*. This assumption is confirmed by the chromatographic results. The populations listed under *N. atomaria* in Table 1 represent both *N. atomaria*

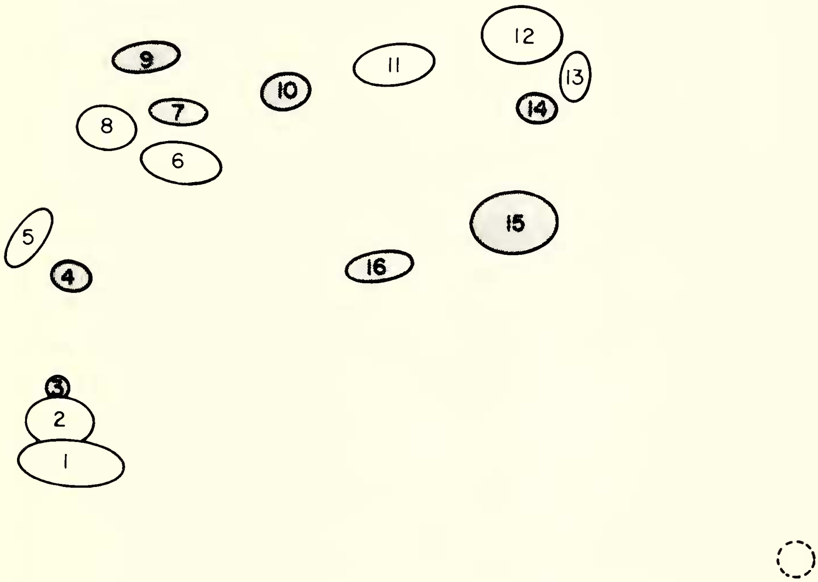

FIG. 1. Composite profile of flavonoid compounds present in corollas of *Nemophila menziesii* s.l. and *N. maculata*. Shaded spots remain dark in UV and ammonia fumes. Light spots appear yellowish-green in UV and ammonia fumes.

Table 1. Presence of Compounds in Populations of Nemophila menziesii Aggregate

Locality	Spot Number 1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
N. atomaria																
Humboldt Co. Berry Summit Rt. 229	+				+	+		+			+	+	+	+		
Marin Co. McClure's Beach	+			+	+	+	+	+	+	+	+	+	+	+		
Sonoma Co. Triniti Rd.	+			+	+	+		+	+	+	+	+	+			
Arnold Drive (*N. liniflora*)	+				+	+			+	+	+	+	+			
Napa Co. Chiles-Pope Valley Rd. 3.2 mi.S. Pope Valley (*N. liniflora*)	+			+	+	+		+	+	+	+	+	+	+		
N. menziesii																
Lake Co. Sawmill Flat	+	+	+		+	+		+		+	+	+	+		+	+
Rt. 175 2 mi. S. Rt. 29	+	+	+		+	+		+		+	+	+	+		+	
Napa Co. Chiles-Pope Valley Road 3.2 mi. S. Pope Valley	+	+	+		+	+	+	+			+	+	+		+	+
Sonoma Co. Sonoma Mt. Rd.	+	+			+	+	+	+			+	+	+		+	+
Arnold Drive	+	+			+	+		+			+	+	+		+	+
Contra Costa Co. Camino Diablo and Vasquez Road	+	+			+			+	+		+	+	+		+	+
San Benito Co. Lonoak Rd. 10 mi. E. Rt. 101	+	+	+		+	+	+	+			+	+	+		+	+
Monterey Co. Jolon-Bradley Rd.	+	+	+		+	+	+	+			+	+	+		+	+
Jolon-King City Rd.	+	+	+		+	+	+	+			+	+	+		+	
Nevada Co. Rt. 49 1.8 mi. N. county line	+	+			+	+		+	+		+	+	+		+	+
Amador Co. ca. 1 mi. S. Jackson City	+	+			+	+	+	+			+	+	+		+	+
Tuolumne Co. Rt. 49 and Mokelumne River	+	+	+		+	+	+	+			+	+	+		+	+
Madera Co. Crystal Springs	+	+	+		+	+	+	+		+	+	+	+		+	+
Bass Lake	+	+	+		+	+		+		+	+	+	+		+	
Fresno Co. 4 mi. S. Alder Springs	+	+	+		+		+	+		+	+	+	+		+	+
Riverside Co. 3.4 mi. S. Idyllwild	+	+	+		+	+	+	+		+	+	+	+		+	

Table 1. (Continued)

Locality	Spot Number 1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
N. integrifolia																
San Bernardino Co. 3.8 mi. E.																
Arrowhead Ranger Station	+	+	+	+	+	+		+	+	+	+	+	+	+	+	+
0.1 mi. E. Arrowhead Ranger Station	+	+	+	+	+	+		+	+	+	+	+	+	+	+	+
Rt. 38 and Skinner Cr.	+	+	+	+	+	+	+	+	+		+	+	+	+	+	
N. maculata																
Madera Co. Bass Lake	+				+	+	+	+			+	+	+	+		
Crystal Springs	+				+	+		+			+	+	+	+		
Fresno Co. 4 mi. S. Alder Springs	+				+	+		+		+	+	+	+			

and *N. liniflora.* On morphological grounds the Arnold Drive and Chiles-Pope Valley Road populations are referable to *N. liniflora,* the others are typical *N. atomaria.* As there are no discernible differences in the profiles of the two taxa, I suggest the proper alignment of *N. liniflora* is with *N. atomaria,* not *N. menziesii.* This is contrary to the suggestions of previous workers (Constance, 1941; Munz, 1959).

Although the number of populations studied in the North Coast Ranges is small, the results substantiate the major taxonomic decisions of earlier workers that two taxa are sympatric in the region. Those plants that appear to be introgressants can usually be assigned to one taxon or the other. For example, plants with *menziesii*-like flowers, i.e., bluish with a white center and colored veins are referable to *N. menziesii,* and, likewise, plants having essentially *atomaria* flowers with blue-edged corolla lobes are referable to *N. atomaria.*

Hybridization Studies

A second line of evidence suggests that introgression may occur, albeit rarely, between *N. atomaria* and *N. menziesii* s.str. Chittenden & Turrill (1926) and Rick (1946) both reported that crosses between plants referable to *N. atomaria* and *N. menziesii* were unsuccessful. Both Chittenden & Turrill (1926) and Rick (1946; pers. commun.) performed many crosses. In no instance were inter-taxon crosses successful. I have performed a small number of crosses between *N. menziesii* s.str. from Sawmill Flat (Lake Co.) and *N. atomaria* from Warm Springs Road (Sonoma Co.). Reciprocal crosses were made. Thirteen crosses using *N. menziesii* as the pollen parent were unsuccessful, but one of seven crosses using *N. atomaria* as the pollen parent was successful, producing a capsule with mature seed. Three selfings of *N. atomaria* were successful indicating that the pollination technique was satisfactory. The few seeds realized from the one successful cross were not germinated. The results suggest that hybridization in natural populations must be a rare event.

Oligolectic Bees on Nemophila

The systematic implications of the following discussion depend on an appreciation of the relationship between an oligolectic bee and its pollen source. An oligolectic species as presently understood is one ". . . in which the individual members of the population, throughout its range and in the presence of other pollen sources, consistently and regularly collect pollen from a single plant species or a group of related plant species, turning to other sources, if at all, only in the face of a local pollen shortage" (Linsley and MacSwain, 1957). The flight period, distribution range, and indeed the whole economy of the bee is tied to that of its host (pollen) plant. The emphasis on pollen source derives from the important role pollen plays in the life of the bee. In solitary bees, including oligolectic bees, pollen is the primary food source of the larvae, the adults utilizing nectar and sometimes pollen as nutrients (Linsley, 1958). Thus the oligolectic bee is tied to its pollen source in the same way a host specific parasite is tied to its host. Because of the specificity of the oligolectic relationships it should be possible to gain new insights with respect to the host plant by studying the bee. Indeed, the presence of an unknown *Cucurbita* in Ecuador was predicted on the basis of the occurrence there of a bee known to be oligolectic on *Cucurbita* (Hurd, pers. commun.).

Four bees are known to be oligolectic on *N. menziesii* s.l. (Cruden, 1972). *Andrena nemophilae* Ribble has been collected on *N. menziesii* s.l. throughout California. This bee is a broadly adapted oligolege in that it collects pollen from all the taxa included in *N. menziesii* s.l. The three remaining species are narrowly adapted oligoleges, i.e., are coadapted to a single pollen source (Cruden, 1972).

Andrena macrocephala Ckll. is widely distributed in southern California, in the Coast Ranges north to Napa and Yolo counties, and in the Sierra Nevada north to Madera Co. Throughout its distributional range *Andrena macrocephala* has been collected primarily on *Nemophila menziesii* (Cruden, 1972). In the North Coast Ranges this bee has been collected on *N. atomaria* (including *N. liniflora*), but where *N. menziesii* and *N. atomaria* occur in mixed populations the bee exhibits a strong preference for *N. menziesii*. For example, at the Chiles-Pope Valley Road population seven of eight females were captured on flowers of *N. menziesii*. A subspecies of *A. macrocephala*, *A. m. tetleyi* Linsley, was collected on *N. integrifolia* at Tetley Park, San Bernardino County (Linsley, 1938). I collected bees from five populations of *N. integrifolia* and failed to see, let alone collect, this bee. Thus the available data suggest that *A. macrocephala* visits *N. menziesii* in preference to both *N. atomaria* and *N. integrifolia* (see also Table 2).

Andrena torulosa LaBerge is found in the Coast Ranges from Santa Clara Co., California, north to Washington Co., Oregon. The distribution of *A. torulosa* mirrors that of its host plant, *N. atomaria* (including *N.*

TABLE 2. FLOWER RECORDS OF BEES OLIGOLECTIC ON NEMOPHILA MENZIESII AGGREGATE

	N. menziesii		*N. atomaria*		*N. integrifolia*	
Bee	Local.	Individ.	Local.	Individ.	Local.	Individ.
Andrena macrocephala	20	216	4	9	2	9
Andrena torulosa	6	32	8	109		
Andrena crudeni	18	93				
Andrena nemophilae	10	76	4	10	1	12

liniflora). Only in the southern North Coast Ranges does *A. torulosa* regularly visit flowers other than those of *N. atomaria*. There it is an important pollinator of non-reflective *N. menziesii* although the bee populations were small when associated with *N. menziesii*. In mixed populations of *N. atomaria* and *N. menziesii* this bee shows a strong preference for *N. atomaria*. At the Chiles-Pope Valley Road population 26 of 27 individuals captured were taken on flowers of *N. atomaria*.

Andrena crudeni LaBerge is an oligolege of *N. menziesii* s.str. and to date is known primarily from reflective populations in the South Coast Ranges from San Luis Obispo Co. north to Santa Clara Co., in the Sierra Nevada from Kern Co. north to Nevada Co., and two locations in southern California. Of the 20 populations I studied this bee was associated with its host plant 18 times. On two occasions, *A. crudeni* was found on flowers of *N. maculata*.

Andrena torulosa and *A. crudeni* are closely related species in subgenus *Nemandrena* whose members all are apparently oligolectic on *Nemophila menziesii* s.l. (LaBerge, 1971; Cruden, 1972). A third species, *A. subnigripes* Viereck, is known only from *N. menziesii* s.str. in Fresno and Tulare counties, California. At the end of the flowering season, when *Nemophila* pollen is scarce, both *A. torulosa* and *A. crudeni* may collect pollen from *Limnanthes* (Limnanthaceae) and *Platystemon* (Papaveraceae). Such late season foraging activity is characteristic of other oligolectic bees (Thorp, 1969).

The floral specificity of *Andrena macrocephala, A. torulosa* and *A. crudeni* corroborate the suggestion from the chemical data that *N. atomaria* (including *N. liniflora*) and *N. menziesii* s.str. are specifically distinct. The failure of Chittenden and Turrill (1926) and Rick (1946) to demonstrate inter-taxon fertility is further evidence for the specific relationship of the two taxa. How then may one explain the obvious evidence of gene exchange between the two taxa?

Variation in Nemophila: An Explanation

The variation observed in present *Nemophila menziesii* and *N. atomaria* may be explained in either of two ways; i.e., introgression subsequent to speciation or gene exchange prior to speciation. Two lines of evidence support introgression as a reasonable explanation. First there is the morphological variation described above which suggests past gene exchange. Second there is evidence from hand pollinations that limited hybridization is possible. Although hybridization is a requisite for introgression, it dos not necessarily result in introgression.

The case of introgression between two subspecies of the house mouse, *Mus m. musculus* and *M. m. domesticus,* in Denmark (Selander, 1970) is particularly relevant. The two subspecies hybridize freely in a narrow band across Jutland producing fertile hybrids but limited gene exchange. The degree of introgression varies from allele to allele and the frequencies of introgressant alleles are usually low. Selander (1970) and others suggest 1) that genomes are co-adapted and 2) that the genetic as well as the external environment is important to co-adapted genes. Thus an allele with a high fitness value in its normal genetic environment is likely to have a low fitness value in a foreign genetic environment.

In comparison with *M. m. musculus* and *M. m. domesticus, N. menziesii* and *N. atomaria* are also genetically and ecologically distinct, indeed more so than in *Mus*. In contrast, hybridization is apparently an uncommon event. If introgression is proportional to hybridization, is it reasonable to attribute to introgression the loss of reflectivity in *N. menziesii* in the North Coast Ranges and the presence of "atomaria" spots in *N. menziesii* in the South Coast Ranges? In contrast to *Mus* an "introgressed" character has replaced a "co-adapted" character in both regions.

An alternative explanation of the observed variation is gene exchange prior to speciation. I suggest that the events that resulted in the geographical isolation of the ancestral *N. menziesii* s.l. population also reresulted in the isolation of the ancestral *Andrena crudeni-torulosa* population. Given today's 1:1 relationship between the bees and plants it seems probable that the ancestral *N. menziesii* s.l. population and *Andrena crudeni-torulosa* population also enjoyed an oligolectic relationship. Geographical isolation also resulted in ecological divergence. Today *N. menziesii* is a member of communities dominated by plants derived from the Madro-Tertiary geoflora whereas *N. atomaria* is a member of communities dominated primarily by species derived from the Arcto-Tertiary geoflora.

What event might explain the geographical separation and subsequent genetic and ecological differentiation of a once continuous population into two discrete entities? I suggest that the incursion of seas over what is now the South Coast Ranges during the Miocene was the event which resulted in geographical isolation of the ancestral plant and bee populations.

During the late Miocene–early Pliocene times the South Coast Ranges composed an archipelago of greater or lesser extent (Axelrod, 1956; Oakeshott, 1971). During these periods the Madro-Tertiary geoflora expanded tremendously. Evidence from Miocene and Pliocene floras (Axelrod, 1956) suggests that the regions probably inhabited by *N. menziesii* s.str. during this period, i.e., the southern Sierra Nevada and the archipelago, were dominated by Madro-Tertiary communities whereas the northern element *(N. atomaria)* lived in regions dominated by Arcto-Tertiary communities.

Given the model of a once continuous population that was geographically separated by a long incursion of seas over the South Coast Ranges, we must hypothesize a population whose floral characters varied clinally over the region of submergence. As evolution proceeded in the resultant populations blue and UV reflectivity were selectively advantageous in the Sierra Nevada populations, whereas white, spotted, non reflective flowers were selected in the North Coast Ranges. The blue-edged corollas in the

North Coast Ranges are thus attributable to "relict", genes in the "atomaria" gene pool. Likewise the "atomaria" spots in the "menziesii" gene pool may be considered relictual. It is perhaps fortuitous that the present day occurrence of variation in UV reflectivity in San Benito and Monterey counties corresponds quite nicely with the Miocene-Pliocene archipelago. It is also in the South Coast Ranges that "atomaria" spots are most prevalent. It seems possible that the Miocene archipelago served as a refugium for intermediate type plants.

The final observation requiring an explanation is the dramatic break between UV reflective and non-reflective populations south and north of the Sacramento River respectively. Obviously, in *Nemophila menziesii* s.l. it is selectively advantageous to be non-reflective north of the Sacramento River. I suggest that in the southern North Coast Ranges *Andrena torulosa* played a role by preferentially visiting non-reflective and low-reflective variants in the *N. menziesii* population as the latter migrated into the North Coast Ranges as today *A. torulosa* is an important pollinator of *N. menziesii* s.str. in the North Coast Ranges.

Summary

Nemophila menziesii s.l. is a species aggregate including *N. menziesii, N. atomaria* and *N. integrifolia.* The three species are morphologically and chemically distinct and *N. menziesii* and *N. atomaria* are reproductively isolated. The specific nature of the three taxa is reflected in the specificity and flower preferences of three bees oligolectic on *N. atomaria* and *N. menziesii.* The close relationship of the three species is suggested by the broadly adapted oligolectic bee *Andrena nemophilae.* I suggest that the incursion of Miocene seas over what is now the South Coast Ranges resulted in the geographical isolation of a once continuous population into two segments, now recognized as *N. atomaria* and *N. menziesii.* As so little is known of *N. integrifolia* I have not included it in my discussion other than to indicate the specific nature of the flavonoid profile from corolla tissue.

Acknowledgments

I wish to acknowledge the encouragement of Dennis Anderson (Humboldt State College) and Jean-Pierre Simon, formerly of Rancho Santa Ana Botanical Garden, in stimulating the preparation of this paper. Lincoln Constance, Lawrence R. Heckard, Thomas Melchert, and Robert Ornduff read the manuscript and their suggestions are greatly appreciated. This report is part of a doctoral thesis submitted to the Graduate School of the University of California, Berkeley.

Literature Cited

Axelrod, D. I. 1956. Mio-pliocene floras from west-central Nevada. Univ. Calif. Publ. Geol. Sci. 33:1–322.

Chittenden, R. J., and W. B. Turrill. 1926. Taxonomic and genetic notes on some species of *Nemophila*. Kew Bull. Misc. Inform., No. 1.

Constance, L. 1941. The genus *Nemophila* Nutt. Univ. Calif. Publ. Bot. 19:341–398.
Cruden, R. W. 1967. Genecological studies in *Nemophila menziesii* H. and A. (Hydrophyllaceae). Doctoral Thesis [Botany] University of California, Berkeley.
————. 1972. Pollination biology of *Nemophila menziesii* with comments on the evolution of oligolectic bees. Evolution (in press).
Daumer, K. 1958. Blumenfarben, wie sie die Bienen sehen. Z. Vergleich. Physiol. 41:49–110.
LaBerge, W. E. 1971. A new subgenus of *Andrena* found in California and Oregon (Hymenoptera:Andrenidae). Pan-Pac. Entomol. 47:47–57.
Linsley, E. F. 1938. Studies in the Andrenidae of North America I. Calif. Acad. Sci. Proc. Ser. 4. 23:263–282.
————. 1958. The ecology of solitary bees. Hilgardia 27:543–599.
———— and J. W. MacSwain. 1957. The nesting habits, flower relationships, and parasites of some North American species of *Diadasia* (Hymenoptera: Anthophoridae). Wasman J. Biol. 15:199–235.
Munz, P. A. 1959. A California flora. Univ. Calif. Press, Berkeley.
Oakeshott, G. B. 1971. California's changing landscapes. McGraw Hill Book Company, New York, 388 pp.
Rick, C. 1946. Studies of natural populations in the *Nemophila menziesii-atomaria* complex. Amer. J. Bot. 33:825 (Suppl. 9a).
Selander, R. K. 1970. Biochemical polymorphism in populations of the house mouse and old-field mouse. Symp. Zool. Soc. Lond. 26:73–91.
Thorp, R. W. 1969. Systematics and ecology of bees of the subgenus *Diandrena* (Hymenoptera:Andrenidae). Univ. Calif. Publ. Entomol. 52:1–146.

NOTES AND NEWS

L. H. Shinners' Collection of Anthophilous Hymenoptera Deposited in Dallas Museum of Natural History.—Dr. Lloyd H. Shinners, the late Director of the Herbarium, Southern Methodist University, Dallas, Texas, had a special interest in pollinating insects. Details of his life have been described by D. S. Correll (Brittonia 23:101–104. 1971) and W. F. Mahler (Sida 4(3):228–231. 1971). During the period 1948–1960, he collected over 8,500 insects, mainly bees and wasps. Virtually all the insects were taken on identified flowering hosts and each insect was assigned a numbered label. As identified insects were returned from taxonomic specialists, he developed a file of insect-flower associations. Three-quarters of the collection is from Texas and provides a rich record of phenological, geographical, and host relationships in an area little studied from the viewpoint of floral biology. Thirteen other states are represented, especially Missouri (11% of specimens). Although the collection was damaged by pests, much unstudied material and the file have been deposited in the Dallas Museum of Natural History. Inquiries for the loan of material should be directed to Mr. Hal P. Kirby, Director, P.O. Box 26193, Dallas Museum of Natural History, Dallas, Texas 75226.—Howell V. Daly, Division of Entomology, University of California, Berkeley 94720.